

## Life History of *Eulemur fulvus rufus* From 1988–1998 in Southeastern Madagascar

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**ABSTRACT** In this study, we compare the life-history patterns of male and female *Eulemur fulvus rufus* based on longitudinal data collected on individuals from two study groups from 1988–1998 in southeastern Madagascar. Mean group size was 9.5 individuals, and groups either contained more adult males than females or equal numbers of both sexes. Females reproduced for the first time between 2 and 4 years of age and reproduced each year, although the mean interbirth interval between surviving offspring was 2.1 years. An average of two adult females reproduced annually in each social group, and age and body weight may positively influence reproductive success. Females also appear to be philopatric but not female-bonded. Young natal males immigrated between 3 and 4.5 years of age and may join a new group within 6–12 months based on the age of emigrants. Once in a social group, they remained until old age, although a male's spatial position in the social group varied with age. Young nonnatal males were members of the social core and had the first opportunity to mate with all estrous females. Older males were peripheral to the social group and mated with females later in their cycle. We hypothesize that group size, the number of females in the group, and individual variation in reproductive success is influenced by several ecological conditions at this site: extreme variability in food availability during reproductive periods, the lack of large food patches, low plant species diversity, and small numbers of important aseasonal food sources such as *Ficus* species. *Am J Phys Anthropol* 108:295–310, 1999. © 1999 Wiley-Liss, Inc.

To better understand and model primate life-history patterns, researchers need long-term data on male and female reproductive patterns, on differential mortality by age and sex, and on the impact these have on the demographic changes within primate populations. Detailed data are now available on these variables from a wide range of anthropoid primate species and have allowed others to conclude that the primate life cycle is not all that unusual compared to other mammals (Koyama et al., 1975; Sade et al., 1976; Dunbar, 1987; Harvey and Clutton-Brock, 1985; Clutton-Brock, 1988; Dobson

and Lyles, 1989; Harvey et al., 1989; DeRousseau, 1990; Cheverud et al., 1992). However, little is known about prosimian primate life history for comparative purposes. The current information that is available regarding

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prosimian life history is based primarily on four species representing three genera (*Lemur catta*: Sussman, 1991; Pereira 1993; *Eulemur fulvus rufus*: Merenlender and Dobson, in press; *Propithecus verreauxi*: Richard et al., 1991; *Propithecus diadema edwardsi*: Wright, 1995).

Based on the work that has been conducted thus far, Malagasy prosimians contrast with anthropoids in significant ways. For example, although a male bias in infant sex ratio is not unusual among anthropoids (Clutton-Brock and Iason, 1986; Dunbar, 1987), the resulting adult sex ratio is usually biased towards females due to higher male mortality (Caughley, 1977; Clutton-Brock et al., 1977; Wolfe, 1984; Dunbar, 1987; Small and Smith, 1986). In contrast, both infant and adult sex ratios are equal or show a male bias in a variety of prosimian species (Petter, 1962; Harcourt, 1987; Sussman, 1991; Richard et al., 1991; Wright, 1995; Nash, 1996; Balko, 1996). In addition, males and females are monomorphic in most prosimian species (Kappeler, 1991; Glander et al., 1992), which may allow for female dominance. Group sizes are also smaller, particularly among arboreal species, and more prosimian species are nocturnal or cathemeral compared to anthropoids (Kappeler and Heymann, 1996).

Originally, researchers hypothesized that these differences were influenced by the extreme energetic constraints that prosimian females face when reproductive. Prosimians were considered to be more energetically stressed during prenatal and postnatal reproductive states than anthropoids because they have an epitheliochorial placentation, short gestation lengths, and basal metabolic rates (BMR) that fluctuate during different reproductive periods (Rasmussen, 1985; Richard and Nicoll, 1987; Richard and Dewar, 1991; Young et al., 1990). However, researchers have demonstrated recently that postnatal reproduction in prosimians may not be as energetically expensive as once believed (Tilden and Oftedal, 1995; Kappeler, 1996). As a result, alternative explanations for the differences observed between prosimians and anthropoids should be considered.

One such hypothesis is that Malagasy primates, particularly frugivores, face more

ecological stress than anthropoids in similar habitats (Kappeler and Heymann 1996; Tilden, 1997). Ecological stress is not clearly defined in these articles, and more concrete observations need to be compiled to substantiate this hypothesis. For example, patch sizes, patch availability, and patterns of fruit production are variables that could influence group size and annual and individual reproductive success. Small group size and the number of potentially reproductive females found in a social group may be strategies prosimians use to cope with increased ecological stress, particularly if reproductive periods coincide with food scarcity periods, if food availability periods are inconsistent, or if food patches are small. However, how prosimian life history and individual reproductive success might be influenced by ecological stress has yet to be determined in wild populations.

The goal of this study, therefore, is to describe changes in group size, survival, mortality, individual reproductive success, and changes in individual spatial relationships in two study groups of red-fronted lemurs (*Eulemur fulvus rufus*) from 1988–1998. These data are used to construct possible male and female life-history patterns and reproductive strategies for this species. Several ecological variables are then compared between Madagascar (at this study site), Asia, Africa, and the New World to identify what ecological variables, if any, differ and how they might influence life history patterns in *Eulemur* species.

## MATERIALS AND METHODS

### Study site

Ranomafana National Park (RNP) was established in 1991 and encompasses 41,000 ha (21°2'–21°25' S, 47°18'–47°37' E) of lowland to montane rain forest in southeastern Madagascar. This region supports 11 primate species in addition to *E. f. rufus* (Wright, 1992). This study was conducted at the Vatoharanana study site, which lies 5 km south from the main RNP research site. Vegetation in this region is characterized as central domain, with Monimiaceae, Cunoniaceae, Lauraceae, and Myrtaceae common canopy trees (Hemingway, 1995). Rainfall

can be quite variable from year to year (2,300–4,000 mm), although the pattern is typically unimodal and rainfall is lowest between May and September (Wright, 1995; Hemingway, 1995 1998; Overdorff, 1996a).

### Study species

Two study groups of red-fronted (or rufous) lemurs (*Eulemur fulvus rufus*) were first habituated in July 1988 by the first author. This species at this site is highly frugivorous (Overdorff, 1993a, 1996a,b), and groups occupy fairly large home ranges (100+ ha) (Overdorff, 1993b) compared to *E. f. rufus* groups on the west coast (Sussman, 1974). Group composition, births, deaths, and migrations have been noted throughout several long-term research projects (see below) and during monthly censuses. Animals in both study groups were darted using the Pneu Dart<sup>TM</sup> capture system (Glander et al., 1991) and given unique colored collar and metal pendent combinations for individual identification. Individual identification also was facilitated by the fact that males and females were sexually dichromatic and individual pelage color varied. Darted individuals were weighed, and standard morphometric measurements were collected (see Glander et al., 1992). An individual's age was determined based on known date of birth or estimated based on tooth wear. The degree of tooth wear on animals of known ages also has been established by comparing dental casts collected on several individuals across a 3 year period (Strait and Overdorff, in preparation). The degree of relatedness for some adult individuals in both social groups between 1988 and 1992 was established by the second author using multisatellite DNA fingerprinting techniques (Merenlender, 1993; Merenlender and Dobson, in press). Four infants born during this study also were included in this analysis.

It has been suggested that males and females in this species are difficult to distinguish from one another in the first few weeks after birth (Pereira, personal communication). In some *Eulemur fulvus* subspecies, including captive red-fronted lemurs, female infants look more like male infants,

while in *Eulemur rubriventer* males infants look more like female infants (Overdorff, personal observation). However, all researchers observing infants in this population recorded that female infants (less than a week old) had no orange tuft on the top of the head, which, in contrast, is pronounced in newborn male infants. Also, the sexual identity of all surviving infants ( $n = 13$  out of 22) did not have to be adjusted as they matured. Finally, in 1996, the body of a 2-week-old infant that had been identified as a female was found, and her sex was confirmed. As a result, we are confident that the identification of an infant's sex during this study was accurate.

### Census

The two main study groups were followed monthly as part of a long-term study on the ecological correlates to group size from July 1988 to August 1989 (Overdorff, 1993a,b, 1996a,b). Other research projects in which these animals were studied intensively included studies on mating behavior (April–June 1990), genetic relatedness and demography (February 1989–1992) (Merenlender, 1993), dental microwear patterns (May–August 1993, 1994, 1995) (Strait and Overdorff, 1995, 1996), and foraging patterns (May–August 1996 to the present) (Overdorff and Erhart, 1998; Erhart and Overdorff, 1998). Two local research guides (P. Talata and A. Telo) also have censused groups 5 days a month between these longer term projects. They noted any changes in group composition and if infants were present. Census activities were extended during September (the birth season) to record as many infant births as possible. These data were used to compile results on individual reproductive success, changes in group size, emigration and migration patterns, and infant and adult sex ratios.

### Ecological variables

Four 50 m  $\times$  5 m transects (representing .1 ha total) were randomly selected from a larger sample of eight transects to compare with data collected by Gentry (1993) on Old World and New World rain forests. Following Gentry (1993), we compiled the following

TABLE 1. Changes in group composition for study groups I and II between July 1988 and August 1995

	Group I		Group II		Total
	Male	Female	Male	Female	
Births	12	2	4	4	22 (23) <sup>1</sup>
Immigrations	2	0	1	0	3
Disappearances	14	2	1	1	18
Group fission <sup>2</sup>	4	1	0	0	5

<sup>1</sup> A new infant was reported in Group I mid-September 1998, sex was not known at this time.

<sup>2</sup> Refers to the number of animals that left the original group when the group fissioned.

data for comparison with comparable rain-forest sites in other regions: basal area, number of plant families and plant species, the number of trees greater than 10 cm diameter at breast height (DBH) (as an estimate of patch size [see Janson and van Schaik, 1988]), and number of *Ficus* species (an important aseasonal food resource for most primates [see Terborgh, 1986]).

Phenological sampling was conducted to determine seasonal food availability patterns from August 1988 to June 1990 (see Overdorff, 1996a; Hemingway and Overdorff, in press), from January 1991 to July 1992 (Hemingway, 1995), and for each summer field season from 1993–1995. Since fruit comprises 50% or more of *E. f. rufus*'s monthly diet, the proportion of individual trees bearing fruit for each month of these study periods was calculated to examine differences in fruit seasonality from year to year and in different reproductive phases. These data were arcsin-transformed, and an ANOVA was used to compare differences in fruit availability among gestation, lactation, and nonreproductive phases.

## RESULTS

### Group size and composition

Changes in group composition occurred due to births, immigrations, disappearances, and a group fission (Table 1). These changes are described in detail in the sections that follow. Overall, study groups ranged from 6–16 individuals (mean group size =  $9.5 \pm 2.9$  individuals not including infants <6 months of age), although group size and growth rate varied by study group. Group I was larger than group II and fluctuated between seven and 16 individuals (mean

group size =  $10.5 \pm 3.3$  individuals) (Table 2). Group I was the only group that did not experience an overall growth rate (0.78), although growth rates exceeded group II's from 1991–1993 (Tables 2, 3). The most dramatic decline in group size occurred when group I fissioned into two permanent subgroups (referred to as group IA and IB) between December 1994 and January 1995. Group II remained more stable and fluctuated between six and ten individuals (mean group size =  $8.1 \pm 1.5$  individuals) (Table 3) but disappeared from the study site after the August 1993 census. Peak group size occurred in 1991 in both study groups.

Solitary uncollared animals ( $n = 22$  [3 females, 19 males]) and pairs ( $n = 18$ ) have been observed throughout the study. Pairs either consisted of one adult male and adult female ( $n = 7$ ) or two adult-sized males ( $n = 11$ ).

### Infant sex ratio and mortality

A total of 23 infants were born from 1988–1998 in both study groups (Tables 1–3) (the most recent 1998 infant is not included in these analyses since its fate and sex are unknown). Overall infant sex ratio was male biased (2.7), although this bias was statistically significant only for group I ( $G = 7.13$ ,  $df = 1$ ,  $P < .008$ ), which produced the largest number of male infants. Overall infant mortality was 40.9%, although infant mortality varied by study group and sex. For example, group I had an overall lower mortality rate (35.7%) than group II (50%). Female infants suffered higher mortality rates (57.1%,  $n = 4$  out of 7) than male infants (33%,  $n = 5$  out of 15;  $G = 6.63$ ,  $df = 1$ ,  $P < .01$ ).

### Male life history

An adult male bias was observed throughout the study (Wilcoxon sign ranked test,  $Z = 3.1$ ,  $P < .002$ ; mean adult males = 5.1,  $SD = 2.0$ , mean adult females = 2.9,  $SD = 0.8$ ,  $n = 17$ ). Group I consistently contained more adult males than females (Wilcoxon sign ranked test  $Z = 2.83$ ,  $P < .005$ ) (Table 2) compared to group II (Wilcoxon sign ranked test  $Z = 1.35$ , not significant) (Table 3).

Three classes of males were identified in this study: natal males, nonnatal males, and old peripheral males. Although the migra-



TABLE 2. Group structure of study group I in November (2 months after the birth season) from 1988–1995<sup>1</sup>

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998 <sup>2</sup>
Group size <sup>3</sup>	9	9	11	16	15	13	12	7	7	7	6
Growth rate	—	0.00	1.22	1.78	1.67	1.44	1.33	0.78	0.78	0.78	0.66
Number of adult males	5	5	5	6	8	10	8	4	3	4	4
Number of adult females	2	4	4	4	3	2	3	2	2	2	2
Number of juveniles	2	0	0	2	3	1	0	1	0	1	0
Number of infants born (number that died in parentheses)	2 (2)	2 (2)	2 (0)	4 (0)	1 (0)	None	1 (0)	None	2 (1)	None	1
Infant M:F ratio	2:0	2:0	2:0	4:0	0:1	0	1:0	0	1:1	0	ND
Adult M:F ratio	2.50	1.25	1.25	1.50	2.67	5.00	2.67	2.00	1.5	2.00	2.00

<sup>1</sup> ND, no data available on infant sex at this time (born mid-September 1998); None, no infants observed.<sup>2</sup> Censused currently through September 1998.<sup>3</sup> Original group size was nine at the beginning of the study in July 1988.TABLE 3. Group structure of study group II in November (2 months after the birth season) from 1988–1995<sup>1</sup>

	1988	1989	1990	1991	1992	1993 <sup>2</sup>
Group size <sup>3</sup>	7	7	9	10	9	9
Growth rate	—	1.13	1.13	1.38	1.13	1.13
Number of adult males	3	3	4	5	4	5
Number of adult females	3	3	3	2	4	4
Number of juveniles	0	1	0	2	1	0
Number of infants born (number that died in parentheses)	2 (1)	2 (2)	2 (0)	2 (1)	none	ND
Infant M:F ratio	1:1	1:1	0:2	1:1	0	ND
Adult M:F ratio	1.00	1.00	1.33	2.5	1.00	1.25

<sup>1</sup> ND, no data available; None, no infants observed.<sup>2</sup> Disappeared after the August 1993 census.<sup>3</sup> Original group size was six individuals at the beginning of the study in July 1988.

tion of a natal male from one group to another has not been directly observed, seven natal males between 3 and 4.5 years of age disappeared from their study group at different times throughout the study. Two natal males left with the portion of the group that fissioned in 1994, and one natal male has remained in his birth group. Two 4–5-year-old male immigrants were observed entering each social group either just prior to or after the May mating season (group I: April 1991 and in March 1995; group II: June 1991). A third male immigrant who was originally a natal male from group II (born 1993) was observed traveling with group I for 9 months between September 1995 and May 1996. The third and fourth authors noted that all immigrants interacted with other group members, did not receive any aggression directed towards them, and were

not peripheral to the group within a month of their arrival.

Overdorff (1998) demonstrated that non-natal males also maintained a distinct spatial relationship with a specific female in the social group (referred to as a male-female dyad). As males aged, they became peripheral, and younger males were more likely to become members of the social core based on the changes in nearest neighbor relationships in group I from 1990 and 1995. For example, ST (a nonnatal male), who was 3 years of age at the beginning of the study, was B's dyad partner in 1995 and was peripheral to the group in 1997. M and N, who had been B's and V's dyad partners, respectively, from 1988–1989 and/or 1990, were peripheral and were often out of sight of the social core during a 2 day follow of group I in 1994.

In each group throughout the study, there were one or two older males (>10 years old) that were peripheral. These males rarely interacted with other group members socially, and each was in poor physical condition. One was blind in one eye, another male had only partial use of his right hand, one lost his testes sometime between the May and June 1994 censuses, and two males developed limps as they aged. Although there was no correlation between age and body weight for adult males (Spearman's rank coefficient  $r = .21$ , not significant,  $n = 16$ ), five males lost weight as they aged and became peripheral to the group (Fig. 1).

#### Female life history and reproductive patterns

No adult female immigrants were observed, and only three adult females disap-

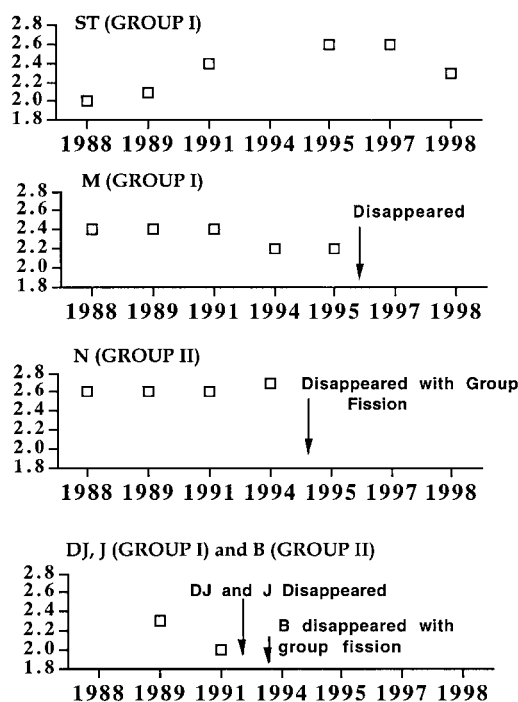


Fig. 1. Relationship between age and body weight (kilograms) for five males in group I (ST, N, M, DJ, and J) and one peripheral male (B) from group II from July 1988 through July 1998. The males' initials are in the upper right-hand corner of each graph and are listed in order of their estimated age from the beginning of the study (ST, 3 years; N and M, 5 years; DJ, J, and B, 10+ years). DJ, J, and B weighed the same during each sampling period in 1989 and 1990, so their data are shown combined into one figure.

peared during the study. A 5-year-old female disappeared from group I with her 6-month-old infant between the March and April 1992 censuses. Another female disappeared in January 1993 when she was 10–11 years old, and an 8-year-old female disappeared from group II in April 1991.

Group I fissioned between December 1994 and January 1995. Based on the identities of the subgroup members (group IB), the fission occurred along a matriline (female S, her son, two of her brothers, and one unrelated male, N). Group IB has not been observed since March 1995, while group IA continues to occupy the study site.

Adult females reproduced almost every year, although individual female reproductive success varied (Table 4). Although more than one reproductive female was present in

a group, only two females reproduced on average each year (mean = 1.7 females, SD = 1.0, range = 0–4 females,  $n = 14$ ). Females reproduced for the first time at 2 ( $n = 1$ ), 3 ( $n = 1$ ), or 4 years of age ( $n = 3$ ), and average interbirth interval was 1.2 years (range 1–3 years, SD = 0.5,  $n = 18$ ). Interbirth intervals between surviving infants, however, were longer (1.9 years, SD = 0.8,  $n = 8$ ) (Fig. 2).

Reproductive females gained weight as they aged (Spearman's rank coefficient  $r = .60$ ,  $P < .03$ ,  $n = 13$ ) (Fig. 3), and the oldest, largest female in each group produced more surviving offspring than other females (Table 4). In general, females appeared to reproduce more surviving offspring when they weighed between 2.3 and 2.6 kg. For example, all four females in group I and two females in group II reproduced surviving offspring when they were within this weight range.

The relationship between group size and infant survival remains unclear given the variation observed between study groups. Overall there was a slight but not significant trend for more infants to survive when groups were larger (Spearman's rank correlation  $r = .35$ ,  $n = 14$ , not significant). However, opposite trends were noted within groups. In group I, the positive relationship between infant survival and group size was stronger but still not significant ( $r = .50$ ,  $n = 9$ ), and in group II fewer infants survived as the group got larger ( $r = -.47$ ,  $n = 5$ , not significant).

### Ecological variables

In Figure 4, the basal area, number of plant families and plant species, patch size (number of trees > 10 cm DBH), and number of fig species found at this study site were compared to similar rain-forest sites from the Old World and New World using data from Gentry (1993). Basal area ( $G = 0.24$ ,  $df = 2$ , not significant) and the number of plant families ( $G = 3.07$ ,  $df = 2$ , not significant) were not significantly different compared to Old World and New World sites. However, there were fewer plant species, large patches (based on DBH), and fig species at this site in comparison (species:  $G = 21.86$ ,  $df = 2$ ,  $P < .0001$ ; patch size:  $G =$

TABLE 4. Individual female reproductive success for group I and II showing the birth rate (proportion of females that gave birth), adjusted birth rate (proportion of infants that survived), the infant sex, and total number of surviving infants each female produced (SI)<sup>1</sup>

	Age <sup>2</sup>	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
<b>Group I</b>												
B	7-8	M (d)	M (d)	M	M	F	None	M	None	M	None	None <sup>4</sup>
V	4	M (d)	M (d)	M	M	None	—	—	—	—	—	—
S <sup>3</sup>	born 1987	None	None	None	M	None	None	None	—	—	—	—
R <sup>3</sup>	born 1987	None	None	None	M (?)	—	—	—	—	—	—	—
MY	born 1992						None	None	None	F (d)	None	Yes <sup>4</sup>
Birth rate		1.00	1.00	0.50	1.00	0.33	0.00	0.50	0.00	0.50		
Adjusted birth rate		0.00	0.00	1.00	0.75	1.00	0.00	1.00	0.00	0.50		
<b>Group II</b>												
CH	5-6	M	M (d)	F	—	—	Gone	Gone				
PR	2	None	F (d)	None	M	None	Gone	Gone				
PB	2	F (d)	None	F	F (d)	None	Gone	Gone				
Birth rate		0.67	0.67	0.67	1.00	0.00						
Adjusted birth rate		0.50	0.00	1.00	0.50	0.00						

<sup>1</sup> (d), died; GONE, entire group disappeared; None, no infants were observed; (?), disappeared; —, disappeared from group.

<sup>2</sup> Estimated age at the beginning of the study.

<sup>3</sup> S and R were born during the September 1987 birth season prior to the study. Merenlender (1993) confirmed that B is R's mother and V is S's mother.

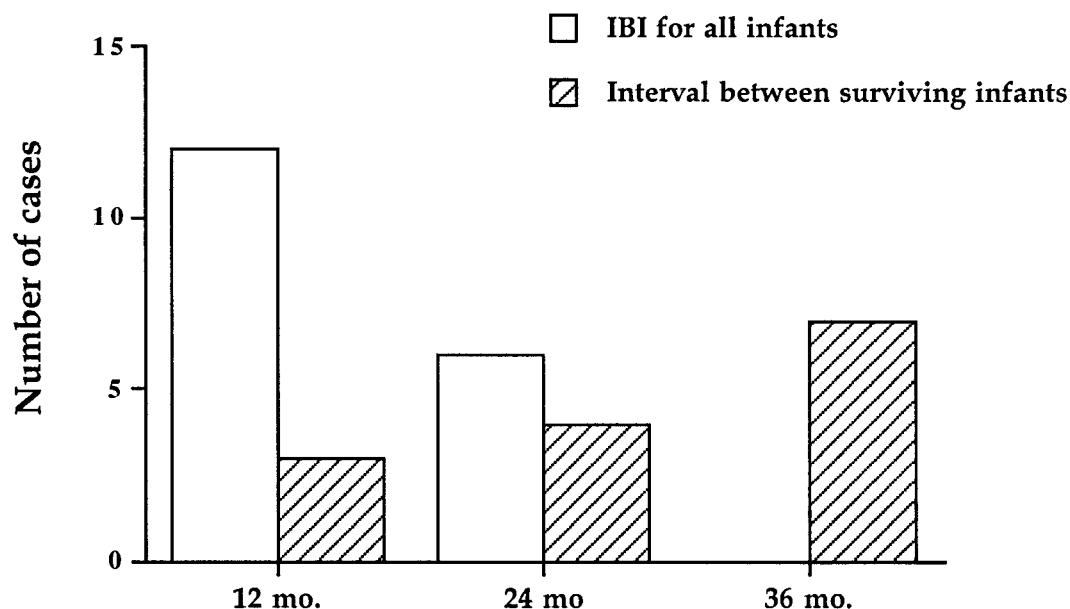


Fig. 2. Interbirth intervals (IBI) for all infants born and for surviving infants for both study groups.

66.2,  $df = 2$ ,  $p < .0001$ ; *Ficus* sp:  $G = 17.3$ ,  $df = 2$ ,  $P < .0001$ ) (Fig. 4).

Patterns of fruit availability during portions of this study are depicted in Figure 5A,B. There was considerable variation in overall fruit availability patterns by reproductive period ( $F = 4.77$ ,  $n = 49$ ,  $df = 14$ ,  $P < .0001$ ). Fruit availability patterns were also variable within periods of lactation ( $F = 8.43$ ,  $df = 3$ ,  $n = 19$ ,  $P < .001$ ) and gestation

( $F = 10.24$ ,  $n = 20$ ,  $df = 6$ ,  $P < .0002$ ) but not nonreproductive periods ( $F = 0.38$ ,  $df = 3$ ,  $n = 8$ , not significant).

## DISCUSSION

### Male life history

It appears that in many respects male *E. f. rufus* follow similar life-history strategies as many cercopithecine males (van Noordwijk

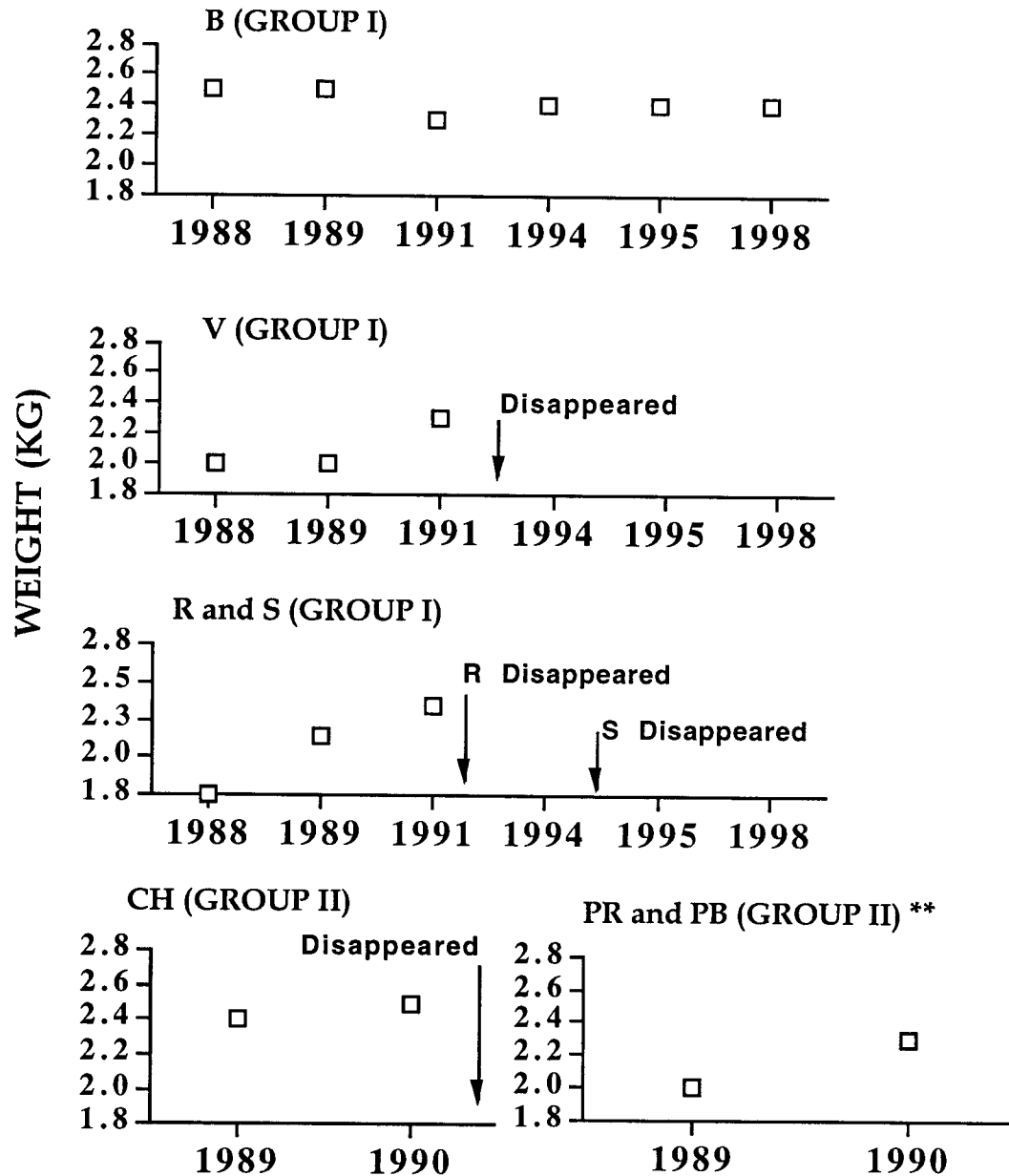


Fig. 3. Relationship between age and body weight for four females from group I (B, V, R, and S) and group II (CH, PR, and PB) from July 1988 through July 1998. Females R and S overlapped in weight gain across the study, as did females PR and PB. Females are listed in order of age from the beginning of the study (B, 7 years; V, 4 years; R and S, 1 year; CH, 5–6 years; PR and PB, 2 years). The time females disappeared is shown by an arrow. \*\*Group II disappeared.

and van Schaik 1985; Sprague, 1992; Alberts and Altmann, 1995). For example, macaque males will migrate between 4 and 5 years of age and attempt to bluff their way

into other groups and achieve top dominance rank after they have reached adult body size. Similarly, male *E. f. rufus* in this study left their study group between 3 and



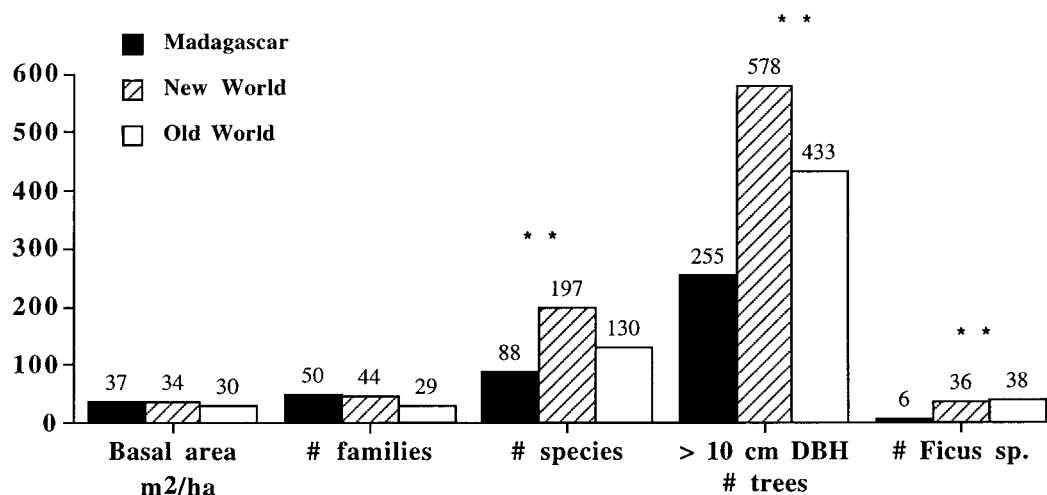


Fig. 4. Comparison of basal area, the number of plant families, number of plant species, patch size (number of trees >10 cm DBH), and number of *Ficus* species for this site in Madagascar and comparable sites from the Old World and New World (Gentry, 1993). \*\* $P < .0001$ .

4.5 years of age when they were sexually mature and had reached full body size. Based on the estimated ages of emigrating males, they may spend 6–12 months being solitary and/or may try several different social groups before they are accepted (see also Merenlender, 1993; Merenlender and Dobson, in press). It also is possible that males migrate in pairs like *L. catta* (Sussman, 1991), given the number of lone male pairs observed throughout this study. Merenlender and Dobson (in press) also demonstrated that there was a high degree of relatedness between two or three males of different ages in these two study groups (and three additional study groups at a nearby study site), and these males were unrelated to any other group member. Consequently, brothers or half-brothers may emigrate into the same group, although not necessarily at the same time. This pattern has been documented in captive populations of the same species and could explain why male emigrants were incorporated quickly into the social groups (Pereira and McGlynn, 1997). How frequently this might occur, however, would depend on the potential number of groups for individuals to migrate into and how many male siblings of the same age occur in the same social group. In wild ring-tailed lemurs which live in

larger social groups than *E. fulvus*, this pattern could not occur on a regular basis since there are not that many brothers of similar ages that could migrate together at the same time (Sussman, 1991; Sauther, 1992).

Nonnatal males do not appear to migrate multiple times once established in a social group and remained in the group until old age. Once established, nonnatal males maintained proximity with specific females and copulated more frequently with females on the first 2 days of their cycle (Overdorff, 1998). These social relationships with females, however, were not exclusive mated pair bonds as implied by van Schaik and Kappeler (1993) since older peripheral males mated with females and one nonnatal male (group I, male N) sired more than one offspring. A nonnatal male can also sire more than one offspring in a group in a given birth season (Merenlender, 1993). However, the process of forming a special relationship with a female may still be a viable reproductive strategy for nonnatal males since five out of the six offspring that Merenlender (1993) obtained blood samples from in these two groups were fathered by nonnatal males (N, M, PR) who were not peripheral.

As nonnatal males aged, they became peripheral to the main social group. Al-

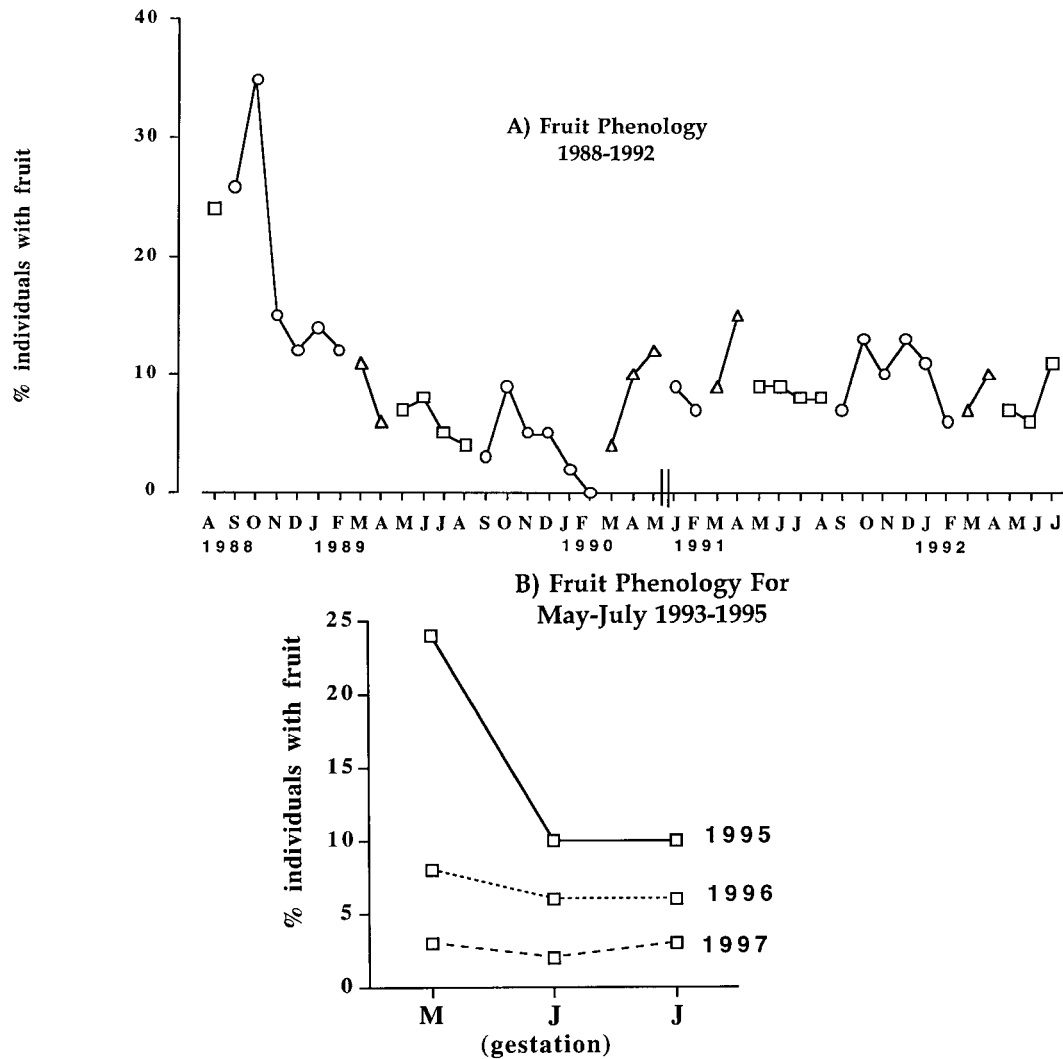


Fig. 5. Fruit availability patterns from August 1988 to June 1990 and January 1991 through July 1992 (A); from May-July 1993, 1994, 1995 (B). Gestation is represented by squares, lactation by circles, and nonreproductive periods by triangles.

though there is no clear-cut dominance hierarchy (see Periera et al., 1990), young nonnatal males may maintain an advantage over older males by being in good physical condition. The majority of peripheral males lost weight, and each one had some physical disadvantage that could impede successful migration into a new group. Consequently, it may be to their benefit to remain associated with a group of familiar animals rather than risk harassment by unfamiliar and/or unrelated animals in a new social group, as often

observed in *Papio* species (Sapolsky, 1996) or risk predation, which is more likely to occur when animals are solitary (Terborgh and Janson, 1986). One peripheral male also fathered an infant (Merenlender, 1993), so older males may still have the opportunity to reproduce occasionally despite their physical disabilities.

Mitani et al. (1996) found that among anthropoids the number of males in multiple male groups was influenced by the number of breeding females. However, they

noted some exceptions to the pattern, such as *Lemur catta* (the only prosimian in their sample) and the Callithricidae, where there were more males in social groups than expected. Since groups in this study also tended towards an equal adult sex ratio or showed an adult male bias, why do *Eulemur* males tolerate additional males, particularly when not every female is successfully reproductive every year? In some primate species, males act as low-cost sentinels for predators (Sauther, 1993; van Schaik and Horsterman, 1994). In this study, the majority of scanning is done by females when resting. However, 80% of scanning activity performed by males was conducted by older peripheral males (Overdorff, unpublished data). While this could be interpreted as a service for the group, it could also be explained by the fact that peripheral males tend to follow further behind the group and, as a result, must increase scanning.

Males also may be tolerated when between-group competition for resources is high. Additional males would effectively increase group size without increasing competition within the group between females. The general (but not significant) trend towards a proportion of surviving infants increasing with group I's size could be interpreted as some support for this hypothesis (Wrangham, 1980; van Schaik, 1983). The slightly negative relationship between surviving infants and group size in group II may reflect some of the possible effects of between-group conflict over food sources since group II was always smaller than group I and was always displaced from food sources by group I ( $n = 32$ ) (Overdorff, unpublished data). This group also eventually disappeared from the study site in 1993. These conclusions are tentative, however, given the small sample size (despite multiple years of data), and further detailed work needs to be conducted to determine how conflict between groups actually influences individual food intake.

The adult male bias observed in this study in infant sex ratio is common in other wild (Richard et al., 1991) and captive prosimian populations (Debyser, 1995). Infant female mortality, however, was higher than infant male mortality, which contrasts to the pat-

tern more commonly observed among anthropoid primates, where males are more fragile and suffer higher mortality rates (van Schaik and de Visser, 1990). One explanation is that infant females may be the more fragile sex and male infant prosimians may be "cheaper" to produce than females. What is currently unknown is if female *E. f. rufus* are more "expensive" energetically to raise than males, a pattern seen in some primates, such as Japanese macaques (Takahata et al., 1995).

More information is needed to determine if females nurse longer, are heavier, are dependent on mothers longer for care, or experience different growth spurts compared to males. Alternatively, the small sample size may have skewed the results since sex differences in overall growth have not been observed in species of similar body size, such as *L. catta* (Pereira, 1993). There is also no reason to suspect that growth rates should vary by sex because male and female *Eulemur* are monomorphic. Consequently, more research is needed to determine the causes of differential mortality in infant *E. f. rufus* and what factors may contribute to a male bias in infancy and adulthood.

#### Female reproductive success and ecological stress

Overall, *E. f. rufus* females in this study had variable reproductive success, which may be related to age and body weight. Although all potentially reproductive females copulated each year, not all females reproduced each year, and one particular female in each group was primarily responsible for the majority of successful births. Interestingly, a similar pattern has emerged from recent data on *Propithecus diadema edwardsi* at this same site (Hemingway, 1995; Erhart and Overdorff, 1998; Overdorff and Erhart, 1998). Although females may not expend any more energy during postnatal reproductive phases compared to anthropoids (Tilden and Oftedal, 1995; Kappeler, 1996), energy expenditure during prenatal reproductive phases still may be critical (Young et al., 1990), especially in regard to the observed variation in food availability during prenatal or postnatal stages.

*E. f. rufus* females reproduced for the first time between 2 and 4 years of age, which is

similar to other Malagasy prosimians, such as *L. catta* (Sussman, 1991) and other populations of *E. f. rufus* at RNP (Merenlender, 1993). Although the sample size was too small to conduct statistical analyses, young (between 2 and 6 years) reproductive females in this study had lower reproductive success and produced fewer infants in successive years than older females (greater than 6 years), which contrasts with patterns observed in many anthropoids (Fedigan and Rose, 1995). Although older females were not more dominant than younger females, there is some evidence that older females have feeding priority over younger females and enter food sources first (Overdorff and Erhart, 1998). Older females often had specific male nearest neighbors that fed near them, and these males prevented other group members from displacing the female while she fed (Overdorff, 1998). Consequently, younger females, particularly natal females who have yet to form strong social relationships with other group members beyond their mothers, may be at a disadvantage in terms of foraging success, which could also influence infant survival. Although four natal females in both social groups (S, R, PR, PB) had lower cumulative reproductive success than older females, several older females also experienced high infant mortality during the first 3 years of the study when they also had a male nearest neighbor dyad partner.

As a result, infant survivorship may be more directly related to maternal weight, which is not an uncommon pattern among other mammals (Gaillard et al., 1992, 1993). Female weight fluctuated throughout the study, but in the year that most infants were produced (1991), females weighed between 2.3 and 2.6 kg. Females who maintained these weights or were heavier (B and CH) also had overall higher cumulative reproductive success. Similar patterns have been recently documented in captive ring-tailed and brown lemurs (Pereira et al., in preparation).

Interbirth intervals were 1 year, which is a common pattern among other prosimian primates in captivity and in the wild (Haring, personal communication). However, the interbirth intervals between surviving in-

fant were longer, slightly over 2 years. This pattern is more typical of larger-bodied prosimians such as the *Propithecus* species (Richard et al., 1991; Wright 1995) and other smaller-bodied anthropoids (Fedigan and Rose, 1995). Because prosimians have extremely seasonal birth and mating seasons (Richard and Dewar, 1991), interbirth intervals will not be affected by the loss of an infant in the previous year, as observed in anthropoids (Fedigan and Rose, 1995). However, infant survivorship in the next year may be influenced by whether or not an infant survived in the previous year. For example, a female produced surviving infants in back-to-back years on only three occasions throughout the study (see Table 4). In all other cases, surviving infants were produced every other year or every 3 years.

The fluctuations observed in group growth, individual reproductive success, and birth rates in rain-forest sites may be related to the dramatic changes in resource availability, as has been observed in other primate populations (Dunbar, 1987; Bernstein et al., 1976; Coelho et al., 1976; Glander et al., 1984; Isbell, 1990). In particular, resource availability in southeastern Madagascar may not be as stable as observed in xerophytic forests of western Madagascar (Jolly et al., 1982; Hladik, 1980; Richard et al., 1991; Sussman, 1991) or as seasonally predictable as once believed (Jolly, 1984). As shown in this study and elsewhere (Hemingway, 1995; Overdorff, 1996b; Hemingway and Overdorff, in press), the phenological patterns of fruit trees were quite variable from year to year and did not appear to be seasonal or predictable annually. Fruit production by plant species and individual trees also fluctuated from year to year. For example, *Chrysopyllum madagascariensis* (which is the second most prominent food item in *E. f. rufus* diets) fruited in August 1988, May 1990, January 1991, November–January 1992, and June 1993 (Overdorff, unpublished data; Hemingway, 1995). Individual *C. madagascariensis* trees also fruited at different times from year to year (Hemingway 1995). Consequently, fluctuations in resource availability of important food items, particularly during the gestation and lacta-

tion periods, may influence infant survivorship and growth rate from year to year. In the early portion of this study when infant mortality was higher, resource availability peaked in late gestation and early lactation (August–September 1988 and 1989). In contrast, peak fruit availability occurred midway through lactation (December) when both groups produced several surviving infants in 1991 (Hemingway, 1995). In other months, fruit availability peaked when animals were not reproductive.

Although the birth season corresponded to peak food availability in August–October 1988, the stress of lactation may be such that infants are most vulnerable at this time despite the apparent increase in food availability. Females also increased their intake of rare food items, such as insects, ants, and flowers, in their diet during lactation (Overdorff, 1993b) as possible additional nutritional supplements. Although more food was available at this time, several other behavioral patterns suggest that group members may actually spend more energy while foraging and that within-group competition may be higher. For example, food patches were smaller and more widely distributed (Overdorff, 1996b), daily path lengths were longer (Overdorff, 1993b), and rates of aggression were higher while feeding (Erhart and Overdorff, 1998). If food is indeed limiting and variable between reproductive periods, why do females tolerate extra group males who would be potential competitors? The critical factor may be the number of reproducing females competing for resources rather than the number of males. Van Noordwijk and van Schaik (1987) found that the overall group size and the number of females competing in the group affected reproductive success negatively in anthropoids. In this study, only two females on average reproduced each year and/or produced surviving offspring. If prosimian females are more energetically stressed during prenatal than postnatal states, food is variable during reproductive periods, and females do not have mechanisms such as female dominance or female bonding as counterstrategies, then groups may be able to support only two or three reproductive females at a time. Older, larger females also may limit the number of

females allowed into a social group by targeting other group members or by promoting a group fission. For example, captive female *Eulemur fulvus* will target young natal females (which had lower cumulative reproductive success in this study) and evict them from social groups (Vick and Pereira, 1989). Unfortunately, this kind of targeting has yet to be directly observed in this population or in other wild populations of related *Eulemur* species (Sussman, 1992; Sauther, 1992; Colquhoun, 1993; Freed, 1996; Curtis, 1997).

This in part may explain the skewed adult sex ratio towards males or why, at best, the number of adult males equals the number of adult females. As mentioned previously, males may also provide some services for females, such as resource defense and predator detection. In addition, larger groups were consistently able to displace smaller groups from food patches (Overdorff, unpublished data). There may, however, be an upper threshold to the number of males a group can support. For example, group I fissioned along a matriline in 1994 when the group had the highest number of adult males. This may be another strategy to minimize competition among females or all group members for food without diffusing kinship and losing group coordination, as has been observed in *L. catta* (Hood and Jolly, 1995).

Terborgh and Janson (1986) hypothesized that the optimal group size for primate species will depend primarily on the size and distribution of food resources within the habitat. Based on the data presented here, the number of plant species, patch size, and the number of potential aseasonal resources such as *Ficus* species (see also Goodman and Ganzhorn, 1997) are lower at this site compared to other sites in Madagascar (Hladik, 1980) and other forests (Gentry, 1993). These more general ecological factors may restrict the diversity of frugivorous fauna, particularly prosimian species, and more specifically place an upper limit on group size for *E. f. rufus* at this site. In contrast, *Eulemur fulvus* species seem to thrive at other sites in Madagascar, particularly in dry forest sites. Sussman (1974) and Rasmussen (personal communication) found high densities of *Eulemur fulvus rufus* and *Eulemur fulvus ful-*



*vus* at their respective study sites. These study populations are also more folivorous, have fewer sympatric species of primates as competitors, and have smaller ranges, although group sizes are comparable to the ones reported in this study. Future study of leaf quality in the Ranomafana area may reveal why our study population of *E. f. rufus* isn't more folivorous, at least seasonally.

In conclusion, it appears that the optimal group size for *E. f. rufus* in the southeastern rain forest is approximately nine animals, and groups contained either an adult bias towards males or an equal adult sex ratio. Group size and the number of reproductive females may influence the birth rate and infant mortality. Older, heavier females tended to have higher cumulative reproductive success than younger natal females, while younger nonnatal males were members of the social core and were more likely to have reproductive opportunities than older males. Males become more peripheral to the social group as they aged. The number of reproducing females in a group, individual variation in female reproductive success, the length of interbirth intervals between surviving offspring, and overall infant survival patterns may be related to ecological stress caused by variability in fruiting patterns between reproductive periods. In addition, further ecological factors, such as the number of plant species, patch size, and diversity of important aseasonal resources such as *Ficus* species, may constrain *Eulemur* group size and influence long-term reproductive success. Further work on other subspecies and similarly sized members of the *Eulemur* genus is needed to confirm if these patterns are typical of this genus or specific to the *Eulemur fulvus* subspecies.

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